ISSN 1062-3590, Biology Bulletin, 2020, Vol. 47, No. 9, pp. 1133–1152. © Pleiades Publishing, Inc., 2020.
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Benthic Communities of Coastal Water Bodies at Different Stages of Isolation from the White Sea in the Vicinity of the White Sea Biological Station, Moscow State University, Kandalaksha Bay, White Sea

M. V. Mardashova[a], *, D. A. Voronov[b, c], and E. D. Krasnova[d]

[a]*Marine Research Center, Moscow State University, Moscow, 119992 Russia*
[b]*Kharkevich Institute for Information Transmission Problems, Russian Academy of Sciences, Moscow, 127051 Russia*
[c]*Belozerskii Institute of PhysicoChemical Biology, Moscow State University, Moscow, 119992 Russia*
[d]*Pertsov White Sea Biological Station, Moscow State University, Moscow, 119234 Russia*
**e-mail: buccinum@mail.ru*

Received November 12, 2019; revised January 20, 2020; accepted March 9, 2020

Abstract—Communities of macrozoobenthos in the White Sea coastal water bodies that have partially or completely lost connection with the sea as a result of postglacial land uplift, are studied. As the degree of isolation from the sea increases, stable vertical stratification with a tendency to meromixis and gradual dilution of seawater provide the conditions for the formation of an unusual composition of macrofauna and succession, from a normal or slightly depleted marine biome to a completely freshwater ecosystem. Data collected in the years 2012–2017 present the macrozoobenthos community of five marine lagoons and four meromictic lakes in comparison with the marine communities of Kislaya Inlet, which connects the two water bodies studied, and with the freshwater lakes of the Kindo Peninsula. The typology of the water bodies was carried out according to the degree of isolation, taking into account the hydrological regime and differences in fauna lists. A naturally determined change in bottom communities occurs as the degree of isolation of the water body from the sea increases. In marine lagoons, regularly flooded by tides, there is a community of *Macoma balthica* (L. 1758)–*Pontonema vulgare* (Bastian 1865) Filipjev 1916, widespread in the marine littoral. In more isolated lagoon-type water bodies with a similar set of species, *Mytilus edulis* L. 1758 and *Mya arenaria* L. 1758 make up a significant share in biomass in addition to *M. balthica*. The populations of the gastropod mollusk *Hydrobia ulvae* (Pennant 1777) are much developed here. Even at this stage, the fauna comprises more littoral eurybionts (*H. ulvae, M. balthica, M. arenaria, M. edulis, Arenicola marina* (L. 1758), *Tubificoides benedeni* (d'Udekem 1855), chironomids, etc.) and less sublittoral stenohaline forms. At the next stage, *H. ulvae* dominates by biomass, and the share of the chironomid *Chironomus* gr. *salinarius* and oligochaete *T. benedeni* increases as well. Insects and their larvae (beetles, chironomids, and other dipterans) settle in shallow areas. In meromictic lakes, where a salt aerobic layer is preserved under the pycnocline, the fauna of the mixolimnion mainly comprises insect larvae, while only a few euryhaline forms remain from the marine fauna, namely, the amphipod *Gammarus duebeni* Lilljeborg 1852 and the chironomid *Ch.* gr. *salinarius*. At the stage of complete isolation from the sea, conditions are anaerobic below the pycnocline and, despite the suitable salinity, there is no marine fauna. In such water bodies, the benthos is represented exclusively by freshwater forms, mainly insects and mollusks. In completely freshwater bodies, chironomids make up the majority of the biomass; each lake has its own set of species, which changes from year to year. In the fresh water of Nizhnee Ershovskoe Lake, the population of *G. duebeni* remains in the part of the lake closest to the sea. The species diversity decreases as the water body is isolated from the sea; the maximum number of species was found in marine lagoons near Sonostrov Island (23–34 species); in Kislo-Sladkoe Lake, 10–15 species are found per survey. In Bol'shie Khruslomeny Lake, the aerobic part of the monimolimnion has a critical salinity and the species diversity is minimal (6–10 species). The number of species increases again after a stable fresh layer appears in the water body. The quantitative characteristics of the macrobenthos change in a similar way. The maximum abundance were noted in marine lagoons; in Kislo-Sladkoe Lake, the average abundance is significantly lower. In the meromictic water bodies with a fresh mixolimnion, the maxima of abundance and biomass are observed in the upper 0.5-m water layer, while in marine lagoons the maxima are located in the depth range of 1.0–2.5 m; in addition, in less isolated water bodies, the maximum biodiversity is observed in deeper layers than in more isolated ones. This layer is characterized by the highest content of dissolved oxygen, and often by supersaturation. The benthos abundance varies greatly in freshwater bodies.

Keywords: isolating water bodies, lagoons, macrozoobenthos, benthic communities, succession, White Sea

DOI: 10.1134/S1062359020090095

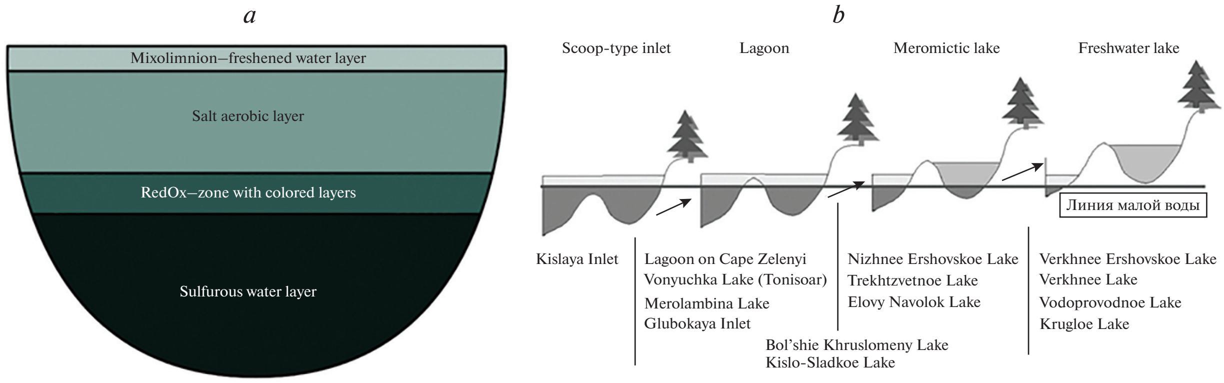

Fig. 1. The water bodies isolated from the White Sea coast: *a,* typical structure of an isolated water body; *b,* a diagram of the evolution of the sea bay as it separates from the sea and the influence of continental runoff increases. Water bodies are divided into groups according to the stage of evolution.

INTRODUCTION

Sea bays and straits may become isolated from the sea and turn into lakes during the process of postglacial isostatic uplift of the coast (Shaporenko, 2004; Olyunina, Romanenko, 2007). In the vicinity of the Pertsov White Sea Biological Station of Moscow State University, a large number of separated water bodies have been found; they have partially or completely lost their connection with the sea, but have not yet turned into freshwater continental water bodies (Krasnova et al., 2013).

Water bodies of this type are found all over the world; different names are used for their designation, depending on the origin and on the classification objectives. In some cases, they are called "relict" [water bodies], for example, Mogilnoe Lake on Kildin Island and the Caspian Sea (Sokolov, 1952). By origin, the White Sea coastal water bodies are also relict, but their age of several hundred years does not allow applying this term to such young formations (Krasnova et al., 2016). An important feature of these water bodies is their stable stratification with a tendency to meromixis, which makes them similar to meromictic water bodies of ectogenic and crenogenic origin with outcrops of salt springs at the bottom (Gorbunov et al., 2007). The strict interpretation of the term "meromictic water body" implies the complete absence of mixing, while the White Sea lakes are disturbed from time to time and at different intervals (Krasnova et al., 2016). The most famous is the relict meromictic Mogilnoye Lake on Kildin Island (Barents Sea), where the balance of sea and fresh waters contributes to evolutionary processes that have led to the formation of specific and unique forms, which is the result of conditions that make the interaction of marine and continental fauna possible (Relict Lake..., 2002; Strelkov et al., 2014). It has been shown that the rate of hydrological and biological evolution of the isolated lagoons differs significantly more than that of the adjacent sea coast (Natural History..., 2014).

The typical structure of the isolated water body includes the upper layer, the mixolimnion, which is subject to wind mixing and is often desalinated (Fig. 1a), but in some lagoons it can be characterized by normal salinity of the surrounding sea. A salty aerobic layer of stagnant water lies below. As a rule, water is not just saturated with oxygen in this layer, but supersaturated up to 300%. The near-bottom water layer is saturated with hydrogen sulfide and is not inhabited by bottom fauna. There is a narrow redox zone between the aerobic and anaerobic layers, which is characterized by a sharp drop in the redox potential; water layers colored by communities of microalgae or prokaryotes may often develop at the layer boundaries (Krasnova et al., 2015).

As the water body becomes isolated, certain changes occur in all its layers. Mixolimnion is gradually desalinated due to continental runoff and precipitation; here, the communities change naturally from marine to euryhaline and brackish water, and then freshwater. The thickness of the salt aerobic layer gradually decreases until it completely disappears, which leads to the formation of a two-layer structure of the water body, and the marine fauna disappears from the lower layers. The influence of the sea on the water body weakens as the transgression of the land goes on. The role of continental runoff increases. The upper layer of the water column is gradually desalinated, and it becomes ever more developed. As a result, the lake is transformed into completely fresh. As early as in the 1930s, G.S. Gurvich pointed out the existence of a historical connection between the scoop-type inlets and lagoons with coastal lakes (Naumov, Martynova, 2016). The meromictic stage may last for hundreds of years (Subetto et al., 2012).

A two-dimensional classification of sea basins was proposed by V.N. Semenov (1988) according to the degree of their isolation, from class I (open water bodies with free water exchange) to class VII (completely isolated from the sea), and size, from type 1 (ocean basins) to type 4 (small bays, less than eight miles long). According to this classification, the Babye More Lagoon, located close to the area of our research (White Sea, Kandalaksha Bay), belongs to class IV–4 (“Inner scoop-type basins”); relict lakes, like Mogilnoe Lake, belong to class VI (“Relict water bodies”), and most of the White Sea isolating water bodies fit between class V–4 (“Upper basins of the inlets, scoop-type water bodies”) and VII (“Fresh lakes of marine genesis”); however, some of them are even smaller in size than provided for by this classification.

Fjords are narrow, deep, and long bays isolated from the sea by a natural bar; as a rule, they have steep rocky shores. This type of water bodies has some similarities with the isolated water bodies of the White Sea (Semenov, 1988). In deep fjords located in the boreal zone, colder water conditions may occur, contributing to the conservation of Arctic fauna. Such phenomena were shown for the Norwegian fjords as early as in the beginning of the twentieth century (Semenov, 1988a). The main differences between the fjords and the isolated water bodies are the relatively greater depths of the fjords, the presence of the usual marine littoral and sublittoral zones with possible displacement of zones, and the loss of parts of the littoral, which is not observed in the isolated water bodies of the White Sea due to their shallow water. The temperature of the bottom water layer of the fjords is below zero; therefore, the accumulation of hydrogen sulfide is impossible (Semenov, 1988a), which is, on the contrary, typical for the lower water layers of the studied isolated water bodies.

Some water bodies at the early stages of isolation belong to the category of scoop-type inlets, which are relatively large and deep water areas separated from the sea by a narrow shallow natural bar, where the tidal regime remains unaltered, if the ratio of the bar depth and the water body depth is less than 1/12 (Gurvich, Sokolova, 1939). The 1/12 model is explained by the disturbance of aeration, leading to the accumulation of bottom hydrogen sulfide (Semenov, 1988a). Most of the isolated White Sea lakes are shallow, and their depths do not exceed 5 m at the deepest point, which does not allow us to apply this criterion to them. Another concept, “lagoon,” is defined as a shallow natural body of water connected to the sea by a narrow strait (which is not necessarily shallow, in contrast to the scoop-type inlet) or isolated from the sea by a ridge of sand, pebbles, etc. (Krasnova et al., 2016). The water bodies of the White Sea at the initial stage of separation correspond to this definition, with the only difference being that the concept of a lagoon does not imply a year-round lack of aeration in the bottom layer, and this is a characteristic feature of coastal meromictic water bodies (Gurvich, Sokolova, 1939; Krasnova et al., 2016). As the coast rises, the distance between the water body and the sea increases, and it may reach 100 m or more; this does not allow us to consider these water bodies as lagoons.

In the southwestern part of the Barents Sea, two salt lakes of the lagoon type (Sisäjärvi and Linjalampi) were surveyed, they connected to the sea by a narrow shallow strait (Deart et al., 2018). These lakes are quite deep (down to 20 m) and are weakly desalinated by continental runoff. The bottom fauna of these water bodies differs insignificantly by its composition and quantitative characteristics from those observed in the apexes of the adjacent bays of the Barents Sea.

In the White Sea, scoop-type inlets have been explored since the end of the nineteenth century; in particular, the Dolgaya Inlet on Bolshoi Solovetsky Island was described by Knipovich in 1893, the Babye More Lagoon has been explored since 1934; Lov Inlet, Palkina Inlet, Kolvitsa Inlet, and Nikolskaya Inlet, as well as Chupa Inlet and Kanda Inlet, attracted attention in the second half of the 20th century (Naumov, Martynova, 2016).

Two small lagoons near the village of Umba were investigated in 1933–1934, including studies of the bottom fauna. At that time, a combination of typical littoral fauna (*M. balthica, Littorina* spp., etc.) with the freshwater and brackish water forms (larvae of caddisflies *Limnephilus* spp. and chironomids) was noted. In general, the community of the lagoon part remote from the bar is characterized as a highly depleted littoral biocenosis with a predominance of *H. ulvae, Gammarus* spp., and rare findings of *M. balthica* and chironomids (Gurvich, Sokolova, 1939).

Babye More Lagoon, which is a scoop-type inlet, was explored during several multidisciplinary expeditions (Comprehensive studies..., 2016). The littoral fauna of this lagoon is significantly depleted in comparison with the marine littoral due to the loss of many infauna species. Actively moving species dominate. The Arctic polychaete *Micronephthys minuta* (Théel 1879) and boreal mollusk *H. ulvae* prevail by abundance, while *Alitta virens* (M. Sars 1835), *M. edulis,* and *M. balthica*, which are characteristic inhabitants of the White Sea littoral zone (Makarov et al., 2016), dominate by biomass. The Velikaya Salma Strait is also classified as a scoop-type water body, although it has a less distinct bar at the entrance (Naumov et al., 2016).

For the scoop-type inlets, there is a characteristic pattern of “displacement” of the zones of the littoral and sublittoral fauna. Moreover, both directions are possible: either the littoral and upper sublittoral forms descend deeper, or the entire deep-sea biocenosis may inhabit the upper sublittoral zone (Semenov, 1988a). In particular, in Babye More Lagoon, the maximum population density of long-lived species (*M. arenaria, M. balthica, Arenicola marina*) is observed in the upper sublittoral zone (Mokievskii et al., 2016).

The isolated water bodies differ from the scoop-type inlets by several parameters. Firstly, the latter are usually deeper than most coastal water bodies isolated from the White Sea and are characterized by the presence of full-amplitude tides. The pycnocline is located deep, and the upper layer of the water column does not differ sharply from those below. They often contain a stagnant bottom zone saturated with hydrogen sulfide.

The lagoons and coastal lakes of Sakhalin Island have been investigated in detail, where various intermediate and transitional forms between marine and freshwater ecosystems have been found (Natural history of Sakhalin..., 2014). The Sakhalin lagoons are very interesting because they represent the whole range from a seawater body to a freshwater one just as observed for the water bodies isolated from the White Sea. According to water salinity, the following categories are distinguished: salt (sea) water bodies (over 22–26‰), brackish waters (from 5–7 to 22–26‰), oligohaline (from 0.01–0.1‰ to 5–7‰), and freshwater (less than 0.01–0.1‰). Therefore, all the White Sea coastal water bodies considered within the present study fall within the range from brackish water to freshwater lakes. Many forms of echinoderms and crustaceans disappear from the Sakhalin brackish water bodies; oligochaetes, mollusks, amphipods, isopods, mysids, decapods, and dipterans are the most significant taxa in oligohaline lakes. Freshwater bodies are close to oligohaline ones by the fauna composition, but the role of other groups of insects (caddis flies, dragonflies, beetles) is more significant here.

Estuarine lagoons are widespread in Kamchatka (Kravchunovskaya, Gorin, 2010). Kamchatka lagoons are very changeable: sand spits that separate them from the sea sometimes grow, then break through, and aquatic communities in them can evolve in both directions, either towards desalination, or towards salination. At the same time, salination in combination with a low level of water exchange causes suffocation phenomena as a result of the acccumulation of hydrogen sulfide (Chebanova, 2013).

Continental meromictic water bodies of the arid zone, such as Shira and Shunet lakes in the Republic of Khakassia (Russia), also have some similarities with the White Sea meromictic water bodies, namely, a pronounced stratification of the water column and a tendency to desalination of the upper layer. In Shira Lake, the thickness of the mixed layer increases simultaneously with its desalination, which affects the composition and quantitative characteristics of the macrozoobenthos negatively (Tolomeev et al., 2018).

Isolated water bodies of the White Sea may serve as model objects in studying the processes accompanying the isolation of a water body both artificially (construction of tidal power plants, fisheries industry) and during natural processes. On the macroscale, the processes occurring during the isolation of such water bodies are similar to those during the formation of the structure of inland seas, and thus they allow extrapolating the knowledge about the cause-and-effect relationships of various natural and anthropogenic phenomena (Naumov, 1979; Semenov, 1988a).

Due to the high rate of coastal uplift (Romanenko, Shilova, 2012) and a specific combination of climatic conditions, the White Sea coastal water bodies have a unique hydrological regime (Kharcheva et al., 2014; Mardashova et al., 2014), providing the conditions for the development of an unusual set of macrofauna (Stolyarov, 2016), in particular, from an impoverished or normal marine biome (Stolyarov, Mardashova, 2017) to completely freshwater communities (Mardashova et al., 2015a). Earlier, there was reported on a decrease in the number of fauna and flora species together with a decrease in the size of the water body as the distance from the ocean increased (Semenov, 1988). The changes in the tidal regime, desalination, pronounced water temperature fluctuations, a decrease in the intensity of the nutrient cycle, and increased ice formation are named as only some factors that decrease the biodiversity of the isolating water body (Semenov, 1988a; Mokievskii et al., 2016). The White Sea is characterized by a high abundance of benthic fauna under the ice, since only the upper littoral zone freezes in winter. Meantime, the influence of freezing extends to greater depths in the isolated water bodies, and most of the fauna descend to the sublittoral zone (Makarov et al., 2016).

Kislo-Sladkoe Lake was the first isolated water body studied near the vicinity of the White Sea Biological Station, Moscow State University (WSBS MSU), where a hydrological structure atypical for the sea bays was discovered (Shaporenko, 2004). Since 2010, studies of this lake and other similar water bodies have been launched at WSBS MSU, which include an inventory of coastal meromictic water bodies in Kandalaksha Bay and monitoring of several of them for hydrological, hydrochemical, and other abiotic parameters (Krasnova et al., 2013). At the same time, the first sampling of the macrozoobenthos began in the water bodies closest to the WSBS MSU, and the first quantitative surveys were carried out in 2014. The aim of this work was to classify the macrozoobenthos communities of thirteen water bodies at different stages of isolation from the sea, considering these

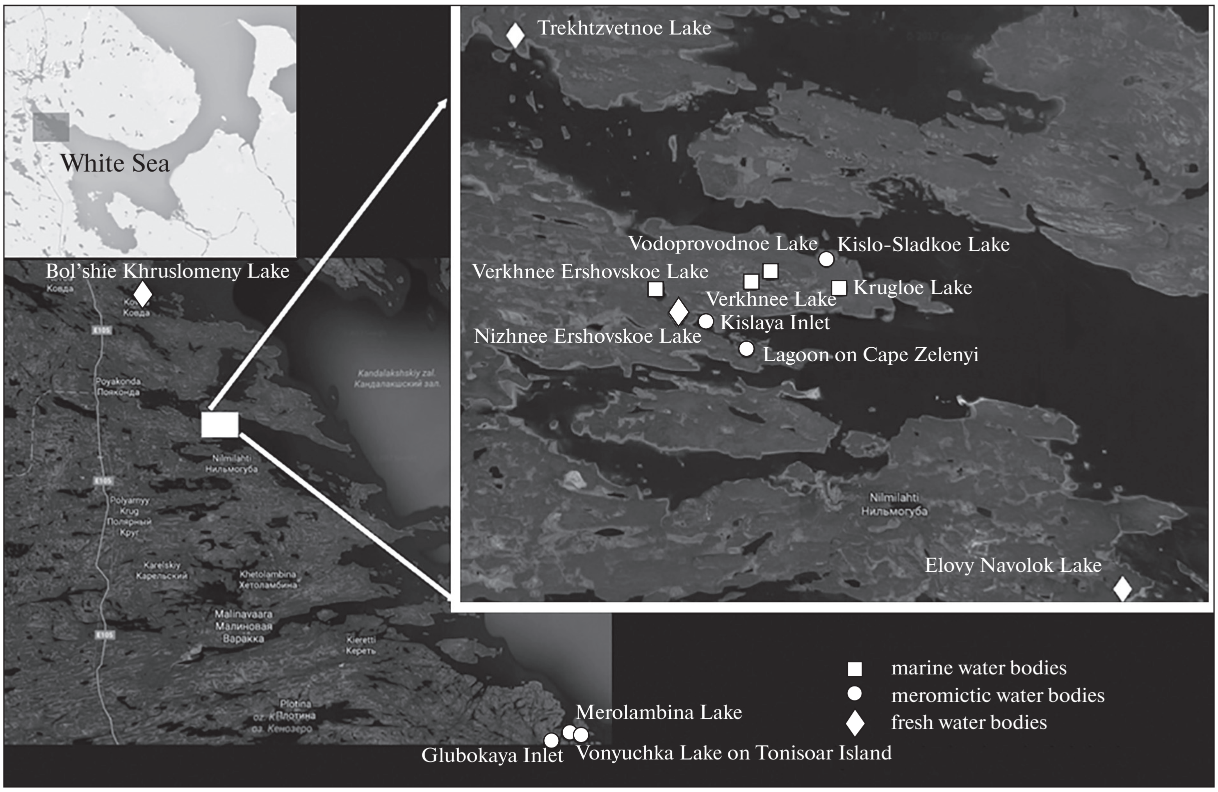

Fig. 2. Map of the location of the lakes studied in Kandalaksha Bay of the White Sea. Circles designate the sea water bodies; rhombuses, meromictic bodies; squares, freshwater.

water bodies with regard to their hydrological characteristics and identifying communities in different functional zones of the water bodies and the development of possible succession series of bottom fauna from the sea bay to the freshwater lake.

MATERIALS AND METHODS

This work was carried out at the Pertsov White Sea Biological Station, Moscow State University, with data accumulated from 2012 to 2017. This article presents information on the composition of the macrozoobenthos communities of four marine lagoons (the lagoon on Cape Zelenyi and three water bodies near Sonostrov Island); salty Kislo-Sladkoe Lake, as well as four meromictic lakes, one of which has a brackish surface layer (Bol'shie Khruslomeny Lake on Olenii Island in the Kovda Inlet), and three lakes with a fresh surface layer (Elovy Navolok, Trekhtzvetnoe, and Nizhnee Ershovskoe lakes). Kislaya Inlet was a reference water body corresponding to the marine environment; two isolated water bodies are connected with this bay, the lagoon on Cape Zelenyi and Nizhnee Ershovskoe Lake. The final freshwater stage in the evolution of the isolated water bodies was studied using the example of three lakes on the Kindo Peninsula, which have also passed through the meromictic stage at different times: Krugloe, Verkhnee, and Vodoprovodnoe lakes (Fig. 1b, Fig. 2, Table 1).

Macrozoobenthos samples were collected with an Ekman-Bergi bottom grab with a capture area of 210.25 cm^2, from a boat and from the shore in summer (June–October), from ice through drilled holes in winter (January–March). Qualitative benthos samples were taken with a bottom scraper and manually from various substrates.

The samples of the bottom sediments were washed on a sieve (1-mm mesh size). In the laboratory, benthic animals were manually removed from the samples. Most of the samples were analyzed alive; in exceptional cases, samples of the washed sediment were fixed with a 7% formaldehyde solution. Invertebrates were identified with the greatest possible accuracy, in most cases, down to the species level, according to the corresponding taxonomic keys (Opredelitel'..., 1948; Gur'yanova, 1951; Ushakov, 1955; Tsvetkova, 1975; Mollusks..., 1987; Opredelitel'..., 1994, 2001; Zhirkov, 2001; Chertoprud, Chertoprud, 2003; Naumov, 2006; Illustrated..., 2009, 2010). The abundance of each taxon was determined alongside with the species identification. Organisms of the same species were weighed together on a Jewelry Scale ML-CF3 with a 1-mg accuracy. The animals that formed

Table 1. Characteristics of the water bodies studied and the amount of material collected

Water body	Coordinates		Parameters		Number of samples	Study years
	N	E	maximal depth	halocline depth		
Kislo-Sladkoe Lake	66.548277	33.134998	4.5	1.0	155	2014–2017
Lagoon on Cape Zelenyi	66.530553	33.095275	6.5	1.5	85	2015–2017
Vonyuchka Lake on Tonisoar Island	66.160829	34.225164	9.5	1.5	12	2017
Merolambina Lake	66.166933	34.184756	8.0	1.0	13	2017
Apex of Glubokaya Inlet	66.167539	34.152208	8.0	–	11	2017
Bol'shie Khruslomeny Lake	66.719274	32.857978	21.0	2.0	16	2017
Elovy Navolok Lake	66.481975	33.279250	5.5	1.0	38	2015–2017
Trekhtzvetnoe Lake	66.592496	32.978618	8.0	1.5	54	2015–2017
Nizhnee Ershovskoe Lake	66.537012	33.059855	2.7	2.0	39	2015–2017
Krugloe Lake	66.542965	33.139459	3.0	–	3	2017
Verkhnee Lake	66.543721	33.097063	3.0	–	10	2015
Vodoprovodnoe Lake	66.545675	33.104521	2.5	–	2	2015
Verkhnee Ershovskoe Lake	66.541773	33.050251	2.5	–	3	2015

around themselves secretory protective structures (calcareous, proteinaceous, and chitinous shells and tubes) were weighed together with these structures; agglutinated protective structures (sand tubes of Pectinariidae, Spionidae, Trichoptera, etc.) were removed before weighing. The biomass corresponds to the wet weight of animals. In order to determine the dominant forms, the functional abundance index was used, calculated as FAI = $N^{0.25} \cdot B^{0.75}$, where N is the species abundance and B is the biomass. The primary data were statistically processed using the Past 3 software (Hammer et al., 2003).

RESULTS

The **lagoon on Cape Zelenyi** is a marine lagoon that communicates with Kislaya Inlet at every tidal cycle. It is subject to small (0.1–0.5 m) tidal fluctuations. The water salinity is higher than in the surrounding sea area from a depth of 1.5 m and down to the bottom.

Forty-seven species of benthic macrofauna were found in the lake (Table 2). The highest frequency of occurrence was typical for the gastropod mollusk *H. ulvae* (89%), chironomid *Ch*. gr. *salinarius* (76%), nematode *Pontonema vulgare* (74%), oligochaete *T. benedeni* (70%), and for the bivalve mollusks *M. balthica* (55%) and *M. arenaria* (43%). The species list comprised marine littoral and sublittoral forms only. The colonies of bryozoans *Electra crustulenta* var. *balthica* Borg 1931 and *Bowerbankia caudata* (Hincks 1877) were found on the boulders of the lagoon bar. The starfish *Asterias rubens* L. 1758 penetrated far into the lagoon, and the ascidian *Molgula manhattensis* (De Kay 1843) was abundant at medium depths. Beetles *Enochrus bicolor* (F. 1792) swam en masse along the lake shores, and the caddisfly *Limnephilus* sp. was found near a small stream flowing into the lake.

The average benthos abundance was 11000 ± 3000 ind./m^2 (Table 3). *P. vulgare* (35%), *H. ulvae* (24%), and *T. benedeni* (17%) were the most abundant species. The biomass was 200±50 g/m^2; bivalve mollusks *M. edulis, M. arenaria,* and *M. balthica* accounted for 83% of the total biomass of the benthos; another 7% was accounted for by *H. ulvae*. The abundance and biomass of the benthos decreased sharply at the 3-m depths, and the contribution of *H. ulvae, Ch.* gr. *salinarius,* and *M. balthica* in functional abundance decreased. The dominant forms here were polychaetes *Heteromastus filiformis* (Claparède 1864), 34%; *Polydora ciliata* (Johnston 1838), 33%; and the oligochaete *T. benedeni*, 16%.

Vonyuchka Lake on Tonisoar Island is a salt lagoon, fenced off from the sea by a natural bar. It is characterized by an increased salinity of the bottom layer (below 1.5-m depth). Tidal fluctuations are 0.5–0.7 m. The lake morphology resembles that of the lagoon on Cape Zelenyi.

In total, 34 species of macrozoobenthos were found, represented exclusively by marine littoral and sublittoral forms. The mysid *Mysis oculata* (F. 1780), bivalve *Hiatella arctica* (L. 1767), and ascidian *Molgula retortiformis* Verrill 1871 were observed here only. The average benthos abundance was 10 000±3000 ind./m^2; nematodes *P. vulgare* (44%) and *Enoplus communis* Bastian 1865 (15%), as well as the oligochaete *T. benedeni* (15%), were the most abundant. The biomass

Table 2. List of species noted in some of the investigated water bodies with a reference to the relative occurrence

Species	Glubokaya Inlet	Tonisoar	Merolambina	Cape Zelenyi	Kislo-Sladkoe	Bol'shie Khruslomeny	Elovy Navolok	Nizhnee Ershovskoe	Trekhtzvetnoe	Verkhnee
Micronephthys minuta			com.							
Mysis sp.	rare									
Mysis oculata		rare								
Molgula retortiformis		domin.								
Pontoporeia femorata			com.							
Hiatella arctica juv.		rare								
Diastylis rathkei	com.									
Molgula manhattensis				com.						
Oedicerotidae gen. sp.			rare							
Paraonidae gen. sp.		sing.								
Lysianassidae gen. sp.	rare	rare								
Caprella sp. juv.				sing.						
Phyllodoce maculata	com.			rare						
Prionospio cirrifera			rare	sing.						
Scoloplos gr. *armiger*	com.	rare		rare						
Mya arenaria	rare		com.	domin.						
Pectinaria koreni	rare	domin.		com.						
Littorina obtusata			rare	sing.						
Littorina littorea	rare		rare							
Littorina saxatilis				rare						
Limapontia cocksi				sing.						
Nemertini gen. sp.	com.	com.		com.						
Tetrastemma sp.		rare								
Poseidon viridis		com.								
Poseidon ruber		com.		com.						
Cephalothrix linearis		rare								
Nais elinguis	rare			rare	sing.					
Macrorhynchus crocea	rare	rare		sing.						
Euchone analis	rare									
Castalia punctata	rare	rare		sing.						
Pygospio elegans			rare	sing.						

Table 2. (Contd.)

Species	Glubokaya Inlet	Tonisoar	Merolambina	Cape Zelenyi	Kislo-Sladkoe	Bol'shie Khruslomeny	Elovy Navolok	Nizhnee Ershovskoe	Trekhtzvetnoe	Verkhnee
Asterias rubens				com.						
Harmothoe imbricata				com.						
Spionidae gen. sp.		sing.								
Crassicorophium bonnellii	com.	abun.		abun.						
Polydora ciliata		abun.		abun.						
Macoma balthica	domin.	abun.	domin.	domin.						
Capitella capitata		abun.		com.						
Heteromastus filiformis	domin.	rare		abun.						
Priapulus caudatus				com.						
Jaera gr. *albifrons*			rare	rare						
Enoplus communis		domin.								
Pontonema vulgare	domin.	domin.	abun.	domin.						
Arenicola marina		domin.		rare	rare					
Pholoe assimilis		com.		rare						
Fabriciola balthica	com.	com.		com.						
Mytilus edulis		rare	domin.	domin.	sing.					
Alitta virens	rare		domin.	com.	rare					
Monocelis fusca				sing.						
Tubificoides benedeni	abun.	domin.	com.	domin.	abun.	rare				
Hydrobia ulvae	domin.	domin.	domin.	domin.	domin.					
Orthocladius gr. *saxicola*		com.		com.	rare		rare			
Chironomus gr. *salinarius*	abun.	abun.	abun.	abun.	domin.	domin.				
Gammarus duebeni	com.		rare	sing.	com.	com.				
Gammarus sp. juv.		sing.								
Polychaeta rest			sing.							
Bowerbankia caudata				rare	rare					
Electra crustulenta var. *balthica*				rare	rare					
Chironomidae gen. sp.	com.	com.	rare	com.	com.	com.	com.	com.	com.	com.
Psilotanypus sp.			com.		rare	com.	com.	abun.	abun.	com.
Acari gen. sp.				sing.	sing.		rare	rare	rare	com.

Table 2. (Contd.)

Species	Glubokaya Inlet	Tonisoar	Merolambina	Cape Zelenyi	Kislo-Sladkoe	Bol'shie Khruslomeny	Elovy Navolok	Nizhnee Ershovskoe	Trekhtzvetnoe	Verkhnee
Nematoda gen. sp.			sing.		sing.		rare	sing.		
Enochrus bicolor				rare	rare					
Ephydridae gen. sp.				rare	com.					
Macroplea mutica					com.					
Limnephilus sp.				sing.	rare					
Polypedilum sp.				rare			rare	sing.	rare	
Limnochironomus gr. *tritomus*				sing.				com.	rare	
Manajunkia aestuarina					sing.					
Enochrus quadripunctatus					sing.					
Aeschna juncea					sing.					
Dytiscidae gen. sp.					sing.					
Corixidae gen. sp. 1					sing.					
Corixidae gen. sp. 2					sing.					
Aedes sp.					sing.					
Pseudochironomus sp.					sing.					
Cladotanytarsus gr. *mancus*					rare		rare	com.	abun.	
Haliplus immaculatus					com.				rare	
Naididae gen. sp.						com.	rare			
Baetis sp.						com.				
Athripsodes sp.						com.				
Microspectra gr. *phaecos*							sing.			
Corixidae gen. sp.							sing.			
Phryganea sp.							sing.			
Pseudochironomus gr. *prasinatus*							domin.	rare		
Gammarus lacustris							com.	com.		
Molanna angustata							rare	rare		
Endochironomus albipennis							rare	abun.		
Endochironomus impar							rare	rare		
Tanytarsus gr. *gregarius*							rare	abun.	rare	
Cryptochironomus gr. *viridulus*							rare	com.	rare	

Table 2. (Contd.)

Species	Glubokaya Inlet	Tonisoar	Merolambina	Cape Zelenyi	Kislo-Sladkoe	Bol'shie Khruslomeny	Elovy Navolok	Nizhnee Ershovskoe	Trekhtzvetnoe	Verkhnee
Cryptochironomus gr. *defectus*							rare	rare	rare	
Lymnaea stagnalis							com.	com.	com.	
Ceratopogonidae gen. sp.							rare		rare	
Caenis horaria							rare		rare	
Pisidiidae gen. sp.							com.	com.	rare	rare
Chironomus gr. *plumosus*							abun.	domin.	domin.	domin.
Anisus sp.							rare	*		rare
Trichoptera gen. sp.							rare			rare
Microtendipes gr. *pedellus*								abun.		
Sialis morio								rare		
Cryptochironomus gr. *anomalus*								rare		
Agrypnia obsoleta								sing.		
Trissocladius sp.								sing.		
Parachironomus sp.								sing.		
Glyptotendipes sp.								sing.		
Mystacides sp.								rare		
Tanypus sp.								sing.		
Oligochaeta gen. sp.								rare		com.
Limnochironomus gr. *nervosus*									rare	
Intercloeon spiniventre									rare	
Parachironomus gr. *pararostratum*									sing.	
Ablabesmyia sp.									sing.	
Bezzia sp.									sing.	
Ischnura pumilio									sing.	
Erpobdella octoculata									sing.	
Tanypus villipennis									sing.	
Phryganea bipunctata									sing.	
Coenagrion sp.									sing.	
Ephemeroptera gen. sp.										com.

Domin., dominant; abun., abundant; com., common; rare, rare; and sing., single specimens.

Table 3. Characteristics of the macrozoobenthos of the water bodies studied

Water body	Number of species	Population density, ind./m^2	Biomass, g/m^2	Dominants by FAI
Lagoon on Cape Zelenyi	47	11000 ± 3000	200 ± 50	*Mya arenaria* (29%), *Mytilus edulis* (25%), *Macoma balthica* (17%), *Hydrobia ulvae* (13%)
Merolambina Lake	20	3000 ± 2000	200 ± 170	*Hydrobia ulvae* (76%), *Macoma balthica* (21%)
Vonyuchka Lake on Tonisoar Island	34	10000 ± 3000	50 ± 10	*Hydrobia ulvae* (52%), *Pontonema vulgare* (24%), *Tubificoides benedeni* (12%)
Apex of Glubokaya Inlet	25	16000 ± 9000	50 ± 20	*Hydrobia ulvae* (63%), *Heteromastus filiformis* (34%)
Kislo-Sladkoe Lake	29	4100 ± 800	50 ± 10	*Hydrobia ulvae* (91%)
Bol'shie Khruslomeny Lake	9	1600 ± 600	6 ± 2	*Chironomus* gr. *salinarius* (98%)
Elovy Navolok Lake	26	1400 ± 1100	3 ± 2	*Pseudochironomus* gr. *prasinatus* (90%)
Trekhtzvetnoe Lake	25	450 ± 200	7 ± 4	*Chironomus* gr. *plumosus* (95%)
Nizhnee Ershovskoe Lake	27	1300 ± 300	10 ± 2	*Chironomus* gr. *plumosus* (55%), *Endochironomus albipennis* (23%)
Krugloe Lake	12	800 ± 300	6 ± 4	*Chironomus* gr. *plumosus* (59%), Pisidiidae gen. sp. (12%)

averaged 50±10 g/m^2; it was represented mainly by the gastropod mollusk *H. ulvae* (26%), polychaete *A. marina* (16%), *ascidian* M. retortiformis (13%), and another polychaete species, *Pectinaria koreni* (Malmgren 1866; 10%). According to the FAI, *H. ulvae* (61%), the nematode *P. vulgare* (21%), and the oligochaete *T. benedeni* (14%) dominated in the upper, less saline layer. Deeper than 1.5 m, the overall population density of the benthos community decreased, and *P. vulgare* (47%), the polychaete *Polydora ciliata* (18%), and *A. marina* (13%) became the dominant forms by FAI.

The apex of Glubokaya Inlet is a salty lagoon with summer stratification and weakened (1 m) tidal fluctuations. It is visually similar to typical sea bays like Kislaya Inlet.

The macrozoobenthos of the water body was represented by 25 marine littoral and sublittoral species. The cumaceous crustacean *Diastylis rathkei* (Kröyer 1841) and sessile polychaete *Euchone analis* (Kröyer 1856) were found here only. The benthos abundance averaged 16000 ± 9000 ind./m^2; the highest abundance was characteristic of the polychaete *Heteromastus filiformis* (41%), *H. ulvae* (38%), and the nematode *P. vulgare* (15%). The average biomass was 50 ± 20 g/m^2; it was mainly composed of *H. ulvae* (37%), the polychaete *H. filiformis* (25%), and the bivalve mollusks *M. balthica* (18%). At the depth range of 0–1.5 m, *H. ulvae* was the absolute dominant by FAI (93%); it was replaced deeper by the polychaete *H. filiformis* (95%).

Merolambina Lake is a lagoon-type estuary; the natural bar isolating it from the sea increased during the construction of a lock for the accumulation of logs during timber rafting. The upper 1-m water layer is diluted with freshwater; the bottom water mass is salty. Tidal fluctuations are 0.3–0.5 m. Despite the desalination of the upper layer, the lake as a whole resembles the rest of the water bodies of Sonostrov Island.

In the lake, 20 species of benthic macroinvertebrates were found, all of them were marine forms. The Arctic polychaete *Micronephthys minuta* and amphipod *Pontoporeia femorata* Kröyer 1842 were found only here. The average abundance of the benthos was 3000±2000 ind./m^2, and *H. ulvae* dominated (85%). The benthos biomass varied greatly as 200±170 g/m^2; the blue mussel dominated (86%). In the desalinated 1-m layer, *H. ulvae* dominated by FAI (97%); in the areas located deeper than 1.5-m depth, it was replaced by *M. balthica* (87%) and juveniles of the polychaete *Alitta virens* (7%).

Kislo-Sladkoe Lake is a sea lagoon with incomplete mixing and a 0.5-m upper water layer diluted with freshwater in spring, in which low salinity is maintained during the hydrological summer. Visually, the water body resembles a sea bay in its northern part, and the southern coast is swampy and resembles the coast of a freshwater water body with vegetation.

In the lake, 29 species of benthic macroinvertebrates were found. Among them, two species of bryozoans were found only on boulders on the natural bar isolating the lake from the sea; these species did not spread far into the water body. The species were represented by marine euryhaline forms with a small contribution of seasonal insect larvae of terrestrial origin. *Hydrobia ulvae* and *Ch.* gr. *salinarius* were the most frequently found species. Oligochaetes *T. benedeni*, larvae of the leaf beetle *Macroplea mutica* (F. 1793), and the crawling water beetle *Haliplus immaculatus* Gerhardt 1877 were also typical species for this water body. Here, a noticeable variety of various insects, especially Diptera, and beetles and Hemiptera, to a lesser extent, was observed for the first time.

The average benthos abundance was 4100 ± 800 ind./m^2, mainly due to *H. ulvae* (78%) and *Ch.* gr. *salinarius* (13%). The biomass was 50 ± 10 g/m^2; in the depth range of 0–3 m, *H. ulvae* contributed more than 90% of the biomass; deeper, *Ch.* gr. *salinarius* dominated, and in some years, *T. benedeni* also was a dominant species.

Bol'shie Khruslomeny Lake is the largest coastal meromictic lake found by us. The lake was artificially isolated from the sea at the beginning of the twentieth century in order to collect freshwater necessary for the operation of the steam engines of a sawmill. However, the surface layer of the lake is desalinated only down to 4–7‰, which corresponds to the ecological level of critical salinity. The lake is subject to regular tides with a level fluctuation of about 0.2 m.

A total of nine species of benthic macroinvertebrates were found in the lake; it was the poorest water body among those studied in terms of biodiversity. It was inhabited by marine euryhaline forms (*G. duebeni, Ch.* gr. *salinarius,* and *T. benedeni*) along with the insect larvae (mayflies and caddis flies). The average benthos abundance was 1600±600 ind./m^2, mainly due to *Ch.* gr. *salinarius* (92% of the total macrozoobenthos abundance). The biomass averaged 6 ± 2 g/m^2; the highest biomass of 26 g/m^2 was registered at a depth of 1 m. Dominant *Ch.* gr. *salinarius* constituted 98% of the total biomass. The shallow zone (0–1.5 m) near the natural bar was lined with large boulders, which made the sampling quite complex. The surface of the stones was covered with a thin layer of detritus, inhabited by a mass of small chironomids and mayflies (Baetidae gen. sp.).

Elovyi Navolok Lake is a meromictic lake with a 1-m fresh top layer and salty near-bottom water layer. Visually, the lake resembles a freshwater body; only the part adjacent to the stream, occasionally exposed to sea splashes, reminds us of the connection of this lake with the sea.

Twenty-six typical fresh water lacustrine species were found. The average benthos abundance was 1400 ± 1100 ind./m^2, and the average biomass was 3 ± 2 g/m^2. One chironomid species, *Pseudochironomus* gr. *prasinatus* dominated both by abundance and biomass (90% and 87%, respectively). The bottom fauna was recorded only for the upper 1-m fresh water layer; some specimens were found in the samples taken down to a 2-m depth.

Trekhtsvetnoe Lake is a meromictic lake with a stable stratification and a 1.5-m fresh upper water layer, the anaerobic zone with sea salinity is located below. Visually, the lake corresponds to the freshwater bodies of the region.

Twenty-five species were found in the lake; all of them were typically freshwater.

The average benthos abundance was 450 ± 200 ind./m^2. *Chironomus* gr. *plumosus* (74%) dominated by abundance, followed by *Cladotanytarsus* gr. *mancus* (9%). On average, the biomass was 7 ± 4 g/m^2, and *Ch.* gr. *plumosus* dominated (97%). Bottom fauna was found down to a depth of 3 m; macroinvertebrates were not found deeper at all.

Nizhnee Ershovskoe Lake is a meromictic lake; most of the water column is fresh, but brackish water remains in the bottom pits. Visually, the water body corresponds to the freshwater lakes of the region.

Twenty-seven species of benthic macroinvertebrates were found in the lake; all of them are typical freshwater representatives of lake fauna. The average abundance was 1300 ± 300 ind./m^2; the chironomids *Endochironomus albipennis* (Meigen 1830; 26%), *Chironomus* gr. *plumosus* (15%), *Tanytarsus* gr. *gregarius* (11%), and other chironomid species (17% in total) were the dominating group. The biomass was low (10 ± 2 g/m^2); *Ch.* gr. *plumosus* dominated (66%), followed by *E. albipennis* (17%). The salt water layer is anaerobic and not inhabited by benthic fauna.

Verkhnee, Vodoprovodnoe, Krugloe, and Verkhnee Ershovskoe lakes are freshwater bodies typical for the region. They are inhabited exclusively by freshwater fauna.

The benthos abundance in Krugloe Lake was 800 ± 300 ind./m^2; chironomids *Ch.* gr. *plumosus* (33%), *Tanytarsus* gr. *gregarius* (23%), and bivalve mollusks of the Pisidiidae family (17%) dominated. The biomass was low, 6 ± 4 g/m^2; dominant *Ch.* gr. *plumosus* accounted for 58%. In Verkhnee Lake, the biomass was 6 ± 3 g/m^2 and *Ch.* gr. *plumosus* contributed to 78%. In Verkhnee Ershovskoe Lake, the benthos biomass was 4 ± 2 g/m^2, and *Ch.* gr. *plumosus* dominated again (72%). In Vodoprovodnoe Lake, no fauna representatives were found, which was also noted earlier (Izvekova et al., 1970).

Kislaya Inlet has good communication with the sea and is inhabited by typical marine fauna. Its apex is partially isolated from the main part of the bay by rapids, which restricts water exchange with the outer water area. In the sublittoral zone of its innermost part, 17 species of macrozoobenthos were found. The total abundance of benthos is 1000 ± 300 ind./m^2, and the total biomass is 100 ± 50 g/m^2. The amphipod *Pontoporeia femorata* (20%), gastropod mollusk *H. ulvae* (20%), and polychaetes *Scoloplos* gr. *armiger* (18%) and *Micronephthys minuta* (15%) dominate by abundance; *M. balthica* (45%), a representative of class Hemichordata *Saccoglossus mereschkowskii* Wagner 1885 (14%), the bivalve mollusk *Astarte montagui* (Dillwyn 1817; 12%), and the polychaete *Pectinaria koreni* (10%) dominate by biomass.

Characteristics of Bottom Sediments

In seawater bodies of the lagoon type (lagoon on Cape Zelenyi, apex of the Glubokaya Inlet, Merolambina Lake, and Vonyuchka Lake on Tonisoar Island), the bottom sediments are represented mainly by the silty–sandy fraction. In the shallows, it is overgrown with *Zostera marina* and *Cladophora sericea*. In the bottom pits, the sediments are more silty, but better washed close to rapids and near the streams. In the lakes with a powerful watercourse (Bol'shie Khruslomeny, Elovy Navolok, and to a lesser extent, in Trekhtzvetnoe and Kislo-Sladkoe lakes), the placement of boulders spread from the natural bar into the depths of the reservoir, making sampling difficult. Kislo-Sladkoe, Trekhtzvetnoe, Elovy Navolok, and Nizhnee Ershovskoe lakes are characterized mainly by silty sediments; freshwater bodies, by silted plant remains and peat. At similar sediments of the White Sea coast, the macrozoobenthos is represented by a rich diverse infauna along with mobile forms.

DISCUSSION

Comparison of benthic communities of the water bodies studied made it possible to identify several regularities: (1) species diversity decreases as the water body is isolated from the sea; (2) the composition of the benthic community depends on the salinity of the layer suitable for the habitation of aerobic fauna; (3) quantitative characteristics of the benthos illustrate the concept of critical salinity; (4) the maximum abundance and biomass of bottom macrofauna in the water bodies, partially isolated from the sea, are observed in the upper layer of the water column; and (5) a zone with stagnant saline water oversaturated with oxygen, which is located below the pycnocline, is especially favorable for marine benthos.

Composition of Communities

As the influence of the sea on the hydrological regime of the water body weakens, a regular change in bottom communities takes place.

The benthic fauna is close to the typical communities of the White Sea in the three salt lakes located on Sonostrov Island and regularly flooded by tides, as well as in the lagoon on Cape Zelenyi. In general, it can be characterized as a community of *Macoma balthica* + *Pontonema vulgare*, widespread in the marine littoral zone (Fig. 3a). Interestingly, a community dominated by *M. balthica* is also characteristic of the Sakhalin lagoons (Natural History..., 2014). In Merolambina Lake, the Arctic polychaete *Micronephtys minuta* is characterized by a high frequency of occurrence, which indicates the similarity of this relatively shallow, 8-m deep lake to the scoop-type inlets (Makarov et al., 2016). The characteristic form *Pontoporeia femorata* is also numerous in this water body, giving a name for the communities of many similar lagoons (Gurvich, Sokolova, 1939); this speics is also noted in Babye More Lagoon (Makarov et al., 2016).

In the lagoon on Cape Zelenyi, in the lower layers of the water column, an even higher salinity is noted than in the adjacent Kislaya Inlet (Krasnova et al., 2013); this water body is characterized by a similar set of species; *M. balthica* dominates here by biomass, followed by *Mitylus edulis* and *Mya arenaria*. Here and in Merolambina Lake, *Hydrobia ulvae* also develops in high numbers. Some excess of the salinity in comparison to the surrounding sea is also noted in Vonyuchka Lake on Tonisoar Island, which is the water body most similar to the lagoon on Cape Zelenyi. *M. balthica* and *M. edulis* along with the polychaete *Alitta virens* dominate here by biomass; a similar community inhabits the littoral of Babye More Lagoon (Makarov et al., 2016). The community of invertebrate macrofauna of these lagoons is similar to that of the parts of the lagoons adjacent to the natural bar near the village of Umba (Gurvich, Sokolova, 1939). The species composition of the macrofauna of the investigated salt lagoons practically repeats the species lists of Ermolinskaya Bay, an open coastal seawater body of the lagoon type (Stolyarov, 2016).

Due to the peculiarities of the bottom contour, Ermolinskaya Inlet is a "germ" of a future isolated water body; it has more littoral eurybionts (*H. ulvae, M. balthica, M. arenaria, M. edulis, Arenicola marina, Tubificoides benedeni,* chironomids, etc.) and fewer sublittoral stenohaline forms (*Pholoe minuta* (F. 1780), *Asterias rubens*, ascidians) already at the current state than the surrounding well-washed lagoons of Kislaya

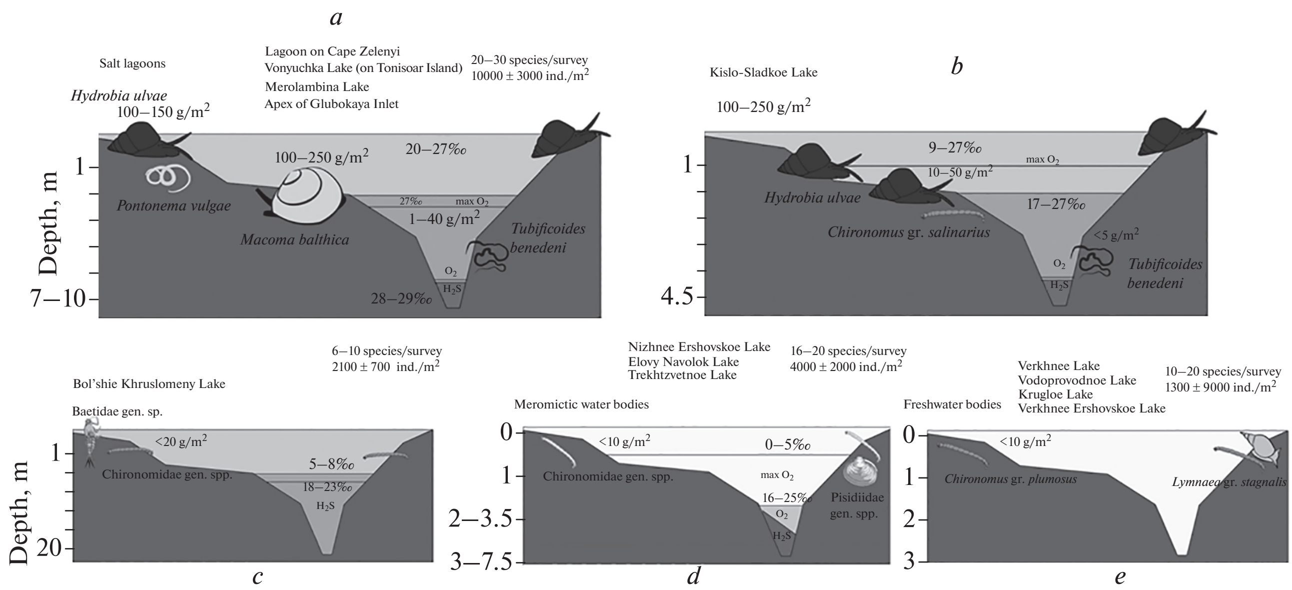

Fig. 3. Scheme of the bottom ecosystem of the isolated water bodies: *a,* a lagoon-type water body (bivalve mollusks predominate, species diversity is relatively high); *b,* Kislo-Sladkoe Lake (the species diversity is reduced, *Hydrobia* and chironomids prevail); *c,* Bol'shie Khruslomeny Lake (the species diversity is the lowest among all water bodies, chironomids predominate); *d,* meromictic water bodies (the species diversity is increasing, chironomids and freshwater mollusks appear at this stage and prevail); *e,* freshwater bodies (species diversity and quantitative characteristics increase even more, mollusks predominate).

Inlet, although the faunas of these two water bodies are very similar in general (Stolyarov, Mardashova, 2017). Widespread opportunistic species (*M. minuta*, Capitellidae gen. sp.) in the Babye More Lagoon and in the other lagoons studied are characteristic of marginal biotopes with a reduced species diversity (Makarov et al., 2016). In the upper water layers, a decrease in the amplitude of tidal fluctuations and freezing of the bottom lead to the disappearance of perennial inactive organisms (bivalve mollusks) and the development of mobile forms, such as amphipods, chironomids, etc. (Mokievskii et al., 2016). The same phenomena are noted in the Sakhalin lagoons (Natural History..., 2014) and are supposedly associated primarily with the features of ice formation.

Kislo-Sladkoe Lake is isolated to a greater extent than the lagoons described above. There are no regular tidal fluctuations here, and the seawater comes only during syzygy tides (Krasnova et al., 2013). Bivalve mollusks are no longer found in the benthos; this significantly decreases the diversity of polychaetes as was observed in artificially isolated water bodies after the construction of the Kislogubskaya tidal power plant in Kislaya Bay, Barents Sea (Shilin, 2009). *H. ulvae* dominates by biomass, and the the chironomid *Chironomus gr. salinarius* and oligochaete *T. benedeni* increase their role (Fig. 3b). This community resembles the biotope of eurybiont deposit feeders in the silted areas of coastal lagoons with low-rate hydrodynamics described earlier (Stolyarov, 2016). A similar community with a predominance of *H. ulvae* and subdominance of other euryhaline forms also develops in lagoon-type water bodies at an earlier stage of isolation (the lagoon on Cape Zelenyi, the water bodies on Sonostrov Island) in the zones corresponding to the upper desalinated layers, as well as in the lagoons near Umba (Gurvich, Sokolova, 1939). A variety of insects (beetles, chironomids, and other Diptera inhabit the shallow areas of the lake. A decrease in the diversity of mollusks and an increase in the proportion of amphibiotic insects is similar to that recorded in the Sakhalin lagoons with a similar salinity range (Natural History..., 2014). In some years, when the upper layer of the water column freshens significantly, larvae of caddis flies of *Limnephilus* spp. appear en masse near the water's edge. The same phenomenon was noted in the lagoons in the vicinity of Umba (Gurvich, Sokolova, 1939).

In Bol'shie Khruslomeny and Elovyi Navolok lakes, the upper layer of the water column is highly freshened, and only a small part of the bottom is covered by the salty aerobic water layer. The fauna of these water bodies is comprised mainly of insect larvae, and only euryhaline forms of the marine fauna remain, namely, the amphipod *Gammarus duebeni* and chironomid *Ch.* gr. *salinarius*. The last species dominates in Bol'shie Khruslomeny Lake (Fig. 3c); the chironomid *Pseudochironomus* gr. *prasinatus* is a dominant form in Elovy Navolok Lake (Fig. 3d).

In the two remaining coastal water bodies studied, the salty water mass (monimolimnion) contains hydrogen sulfide throughout the entire column; there are no conditions for the habitation of marine or euryhaline forms. Therefore, the benthos is represented only by freshwater forms, mainly by insects and mollusks of terrestrial origin. Only in the meromictic Nizhnee Ershovskoe Lake does the population of *G. duebeni* remain in the part of the water body closest to the sea.

Chironomids make up the basis of the biomass in Nizhnee Ershovskoe and Trekhtzetnoe lakes; each lake has its own set of species, which changes from year to year. For example, an outbreak of *Endochironomus albipennis* was recorded in Nizhnee Ershovskoe Lake in 2015, which was not found in any of the lakes en masse; in the summer of 2017, it was *Ch.* gr. *plumosus*. In the fresh mixolimnion of Trekhtzetnoe Lake, macrofauna is typically freshwater: here, chironomids predominate, especially *Ch.* gr. *plumosus*.

In terms of fauna, freshwater bodies are generally similar to the fresh mixolimnion of meromictic lakes; however, the diversity of insects (dragonflies, beetles, Hemiptera, Diptera) is higher there, and bivalve mollusks make a greater contribution to the biomass (Fig. 3e), which is consistent with the data of previous researchers (Izvekova et al., 1970).

The composition of the fauna changes in accordance with the salinity of the upper water layer (Fig. 4). The saltiest water bodies, the lagoon on Cape Zelenyi (23.4±0.04 psu), Vonyuchka Lake on Tonisoar Island (21.1±0.05 psu), and Glubokaya Inlet (17±7 psu) are characterized by fauna close to typical of the White Sea. Merolambina Lake, despite the powerful fresh runoff and the corresponding freshening of the upper layer of the water column, has a composition and quantitative characteristics similar to the previous three water bodies. Kislo-Sladkoe Lake (16.7±0.7 psu) already differs significantly both by species composition and by the quantitative characteristics of the benthos, which both tend to decrease. The trend continues further on; Bol'shie Khruslomeny Lake (5.3±0.5 psu) is characterized by the poorest fauna among the water bodies studied. Meromictic water bodies, i.e., Elovy Navolok (0.5±0.3 psu), Nizhnee Ershovskoe (0.2±0.05 psu), and Trekhtzetnoe lakes (0.5±0.1 psu) already fully correspond to freshwater water bodies by the fauna composition.

The same order is tracked for the isolated water bodies according to the specific catchment index, which is the ratio of the catchment area to the lake area (Krasnova et al., 2016). The most isolated and saline body of water, the lagoon on Cape Zelenyi, has the lowest specific catchment index (7.2). Kislo-Sladkoe Lake has a higher indicator of 9.72; in Trekhtzvetnoe and Nizhnee Ershovskoe lakes, this index is the highest (19.8 and 15.1, respectively).

Quantitative characteristics

The maximum number of species is observed in the lagoons of Sonostrov Island (23–34 species per survey); in Kislo-Sladkoe Lake, 10–15 species per survey. In Bol'shie Khruslomeny Lake, the aerobic layer has the critical salinity, and the number of species is minimal (6–10); when a stable freshwater layer appears in the water body, the species diversity increases again in accordance with the classical concept of critical salinity (Khlebovich, Aladin, 2010). The same is observed in the oligohaline lagoons of Sakhalin Island (Natural History..., 2014). In general, the partial isolation of the water body at the early stages leads to a slight decrease in the species diversity, which is aggravated by the increase in stagnation and siltation of the littoral zone, both during natural processes and during artificial isolation of the water body (Marfenin et al., 1995). In fjords and scoop-type inlets, the decrease in diversity is less pronounced and more typical for the littoral zone also due to their large size (Makarov et al., 2016; Deart et al., 2018). The changes become more pronounced and begin to affect the sublittoral zone as the isolation progresses (Gurvich, Sokolova, 1939).

The quantitative characteristics of the macrobenthos fauna change similarly. The maximum abundance was recorded in marine lagoons (up to 100000 ind./m^2), on average, about 10 000 ind./m^2 (Grachev et al., 2015), which corresponds to or is only slightly less than in open areas of the littoral (Makarov et al., 2016). In Kislo-Sladkoe Lake, the average abundance is significantly lower, about 3000 ind./m^2 (Buvalyi et al., 2015; Krylova et al., 2015). In adjacent areas of the littoral zone, the abundance of benthic invertebrates is usually slightly lower than in marine lagoons, varying from 500 to 3000 ind./m^2. Similar values are typical for the littoral of Babye More Lagoon (Makarov et al., 2016). The lowest values of the benthos abundance are noted in meromictic water bodies, constituting about 1000 ind./m^2 (Bol'shie Khruslomeny, Elovy Navolok, and Trekhtzvetnoe lakes). Freshwater bodies vary greatly in the benthos abundance, from 1300 up to 9000 ind./m^2 (Kosenkov et al., 2015).

The maximum biomass of 200–300 g/m^2 is observed in the marine littoral of open lagoons (Stolyarov, Mardashova, 2017), which is quite consistent or even slightly exceeds the productivity of the macrozoobenthos in the White Sea littoral zone (Makarov et al., 2016). A slightly lower biomass (50–170 g/m^2) is observed in the lagoons at the early stages of isolation (Grachev et al., 2015; Mardashova et al., 2015b), 20–60 g/m^2, in Kislo-Sladkoe Lake (Buvalyi et al., 2015; Mardashova et al., 2015). The biomass in large scoop-type inlets, for example, in Babye More Lagoon (50–60 g/m^2), is characterzed by an intermediate position between the sea lagoons and Kislo-Sladkoe Lake

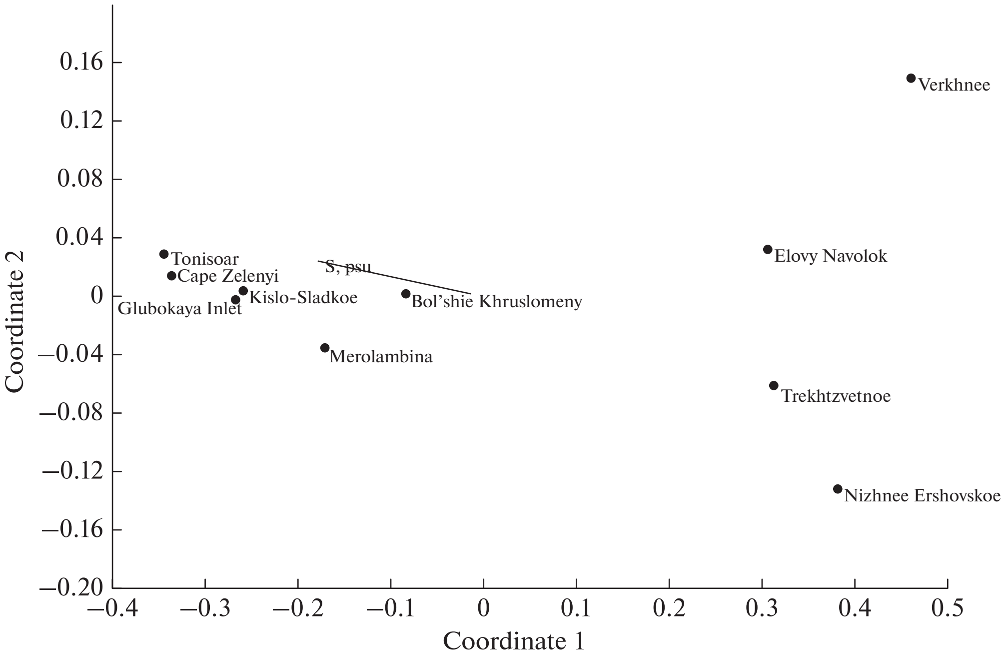

Fig. 4. Ordination of water bodies by the method of multidimensional scaling. The water bodies diverge according to the factor of the salinity axis of the upper layer of the water column.

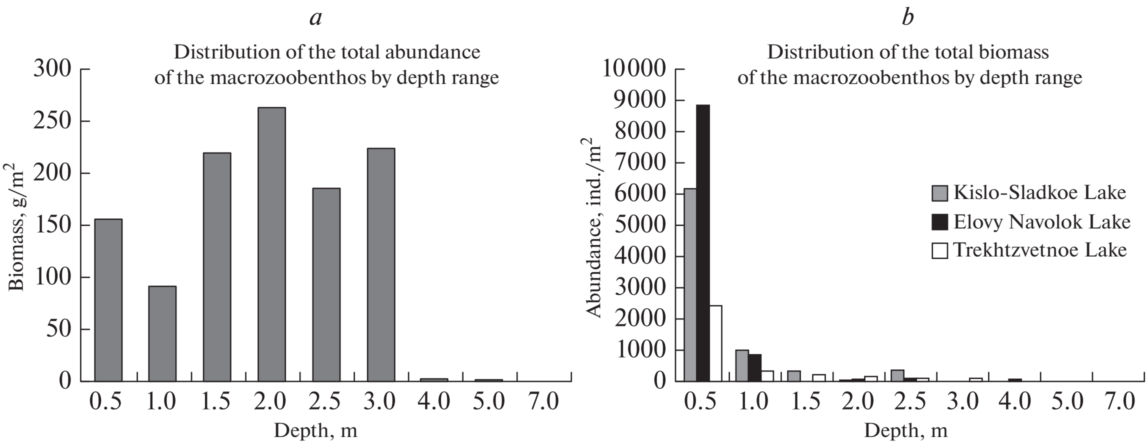

Fig. 5. Quantitative characteristics of the macrozoobenthos: *a,* distribution of the total biomass of the macrozoobenthos over depths in salt lagoons using the example of a lagoon on Cape Zelenyi (the maximum biomass is observed in the zone with an increased oxygen content and falls, not in the uppermost water layer, in contrast to meromictic and freshwater water bodies); *b,* distribution of the total abundance of macrozoobenthos by depths using the example of the three water bodies.

(Makarov et al., 2016)). An even lower biomass (10–40 g/m^2) is noted in freshwater and meromictic lakes (Kosenkov et al., 2015; Mardashova et al., 2015a). By the example of the Sakhalin Island water bodies, it is shown that the quantitative indicators of the benthos are often higher in lagoons than in the surrounding coastal area (Natural History, 2014). In the case of the White Sea lagoons, this is true only for the very initial stages of isolation. The biomass of the benthos reaches 200–300 g/m^2 only in the lagoon on Cape Zelenyi and in Merolambina Lake in the clusters of bivalve mollusks. The average benthos biomass of 114±9 g/m^2 is observed in Kislaya Inlet, adjacent to the lagoon on Cape Zelenyi (Stolyarov, Mardashova, 2017).

In the water bodies with fresh mixolimnion, the maximum abundance and biomass is characteristic of the upper 0.5-m water layer (Kosenkov et al., 2015; Fig. 5), while in sea lagoons it is located in the depth range of 1.0–2.5. In less isolated water bodies, it is located deeper than in more isolated ones. Interestingly, the maximum of the quantitative characteristics is a feature of the layer with the highest oxygen saturation. A.N. Naumov et al. (Naumov et al., 2016) suggested that the oxygen regime might possibly explain secular changes in the fauna, at least in the deep-sea Arctic complex.

The localization of the freshwater forms in the uppermost water layers and a significant decrease in the benthos diversity and abundance in the underlying zones was also noted in the freshwater lakes of Velikii Island, White Sea. For example, in Maloe Kumyazh'e Lake, the average benthos abundance in the littoral zone is 900 ind./m^2, biomass, 2 g/m^2, which is consistent with our data in the upper 0.5-m layer of freshwater bodies, while at depths exceeding 3 m these values are 60 ind./m^2 and 0.2 g/m^2, respectively (Izvekova et al., 1970). The freshwater bodies studied by us have shallower depths than the lakes of Velikii Island; so we tend to explain this by the lesser variety of forms and an even greater localization of the fauna along the coastline. In water bodies of similar size, the number of species (6–27) corresponds to the data obtained earlier, when the predominance of chironomids was noted in Verkhnee Lake (Izvekova et al., 1970). We have not yet compared fresh lakes with isolated water bodies sufficiently in detail to reach a conclusion on the completeness of the species lists. However, it is obvious that the most abundant chironomid species may vary from year to year independently in different water bodies.

CONCLUSIONS

The communities of the macrozoobenthos in the water bodies isolated from the White Sea change in the course of the evolution of the water body in a similar way and in accordance with the change in the hydrological regime. As the water body becomes isolated, the littoral and sublittoral fauna becomes impoverished, first, primarily due to infauna. Then the fauna is replaced by eurybiontic forms, after which the species diversity begins to increase again, due to the development of insect larvae, and, finally, there is a total replacement of the marine diversity by the freshwater forms.

The species composition of the macrozoobenthos is preconditioned by the ratio of the influence of the coastal runoff and the sea on the hydrological structure of the water body and depends on the salinity of the layer suitable for the habitation of aerobic fauna. The quantitative characteristics of the benthos in the series of isolated water bodies illustrate the concept of critical salinity. The vertical distribution of the benthos is related to the hydrological zoning of the water body. In meromictic water bodies with a fresh mixolimnion, the maxima of abundance and biomass are observed in the upper 0.5-m water layer, while in marine lagoons, the maxima are located in the depth range of 1.0–2.5 m, where the highest content of dissolved oxygen is observed, reaching supersaturation quite often. Thus, the zone most favorable for the marine benthos is that with stagnant salt water, oversaturated with oxygen, and located below the pycnocline. At the early stages of isolation, the population density and biomass of the benthos may first increase with depth and only then decrease; at later stages, the benthos communities are more and more confined to the mixolimnion.

The typological series of the water bodies at different stages of isolation from the parent water body may be extended on a macro-scale to the White Sea, which can be considered as a kind of scoop-type bay of the Barents Sea. The salinity of the White Sea is reduced in comparison with the normal oceanic salinity and is comparable to the values of the brackish lagoons of Sakhalin. This order of isolation corresponds to the loss of many forms of echinoderms, crustaceans, and other groups from the biocenosis, which is observed both in the Barents Sea–White Sea series and in the comparison of the marine and brackish water lagoons of Sakhalin (Natural History..., 2014).

ACKNOWLEDGMENTS

The authors are grateful to the crew of R/V *Professor Zenkevich,* namely, captain Yu.I. Kozhukhov and marine engineer E.Z. Gabaidulin. Special thanks go to S.N. Lomovtsev, V.V. Sivonen, and the administration of the WSBS MSU for the opportunity to work at the biological station; and V.A. Spiridonov and V.O. Mokievskii, for providing the help with the sampling gear and plentiful advice.

FUNDING

This work was supported by the Russian Foundation for Basic Research, project no. 19-05-00377.

COMPLIANCE WITH ETHICAL STANDARDS

Statement on the welfare of animals. This article does not contain any studies involving animals or human participants performed by any of the authors.

Conflict of interest. The authors declare that they have no conflict of interest.

REFERENCES

Buvalyy, S., Garmaeva, S., Mardashova, M., Krasnova, E., and Menshenina, L., Macrobenthos composition at the shoreline of Kislo-Sladkoye Lake, separating from the White Sea, *EARSeL eProceedings*, 2015, vol. 14, suppl. 1, pp. 63–70.

Chebanova, V.V., Dynamics of distribution and abundance of macrozoobenthos in the Nerpichye–Kultuchnoye lake system (the Kamchatka River estuary), *Issled. Vodn. Biol.*

Resur. Kamchatki Sev.-Zapadn. Chasti Tikhogo Okeana, 2013, vol. 31, pp. 89–97.

Chertoprud, M.V. and Chertoprud, E.S., *Kratkii opredelitel' bespozvonochnykh presnykh vod tsentra Evropeiskoi Rossii* (A Short Guide to Freshwater Invertebrates in the Center of European Russia), Moscow: MAKS Press, 2003.

Deart, Yu.V., Pereladov, M.V., Spiridonov, V.A., Antokhina, T.I., Rzhavsky, A.V., and Britayev, T.A., Soft Bottom Communities in Marine Lakes Sisjajarvi and Linjalampi (Barents Sea), *Dokl. Biol. Sci.*, 2018, vol. 478, no. 5, pp. 29–32.

Gorbunov, M.Yu., Umanskaya, M.V., and Krasnova, E.S., Characteristics of abiotic conditions in the ecosystem of the Nizhnii Pond of the Botanical Garden of Samara University, *Samar. Luka: Probl. Region. Glob. Ekol.*, 2007, nos. 1–2 (19–20), pp. 131–143.

Grachev, D.I., Lyalina, E.M., Sitnikov, K.M., Trifanov, P.V., Krylova, M.A., and Mardashova, M.V., Quantitative distribution of mollusks and other mass invertebrates by depths in the lagoon on Cape Zelenyi (White Sea), in *Vodnye resursy, ekologiya i gidrologicheskaya bezopasnost': Sbornik trudov IX Mezhdunarodnoi nauchnoi konferentsii molodykh uchenykh i talantlivykh studentov, 30 noyabrya 2 dekabrya 2015 g* (Water Resources, Ecology, and Hydrological Safety: Proceedings of the IX International Scientific Conference of Young Scientists and Talented Students, November 30–December 2, 2015), Moscow, 2015, pp. 24–27.

Gur'yanova, V.F., *Bokoplavy morei SSSR i sopredel'nykh vod (Amphipoda–Gammaridea)* (Amphipods of the Seas of the USSR and Adjacent Waters (Amphipoda–Gammaridea)), Moscow: Akad. Nauk SSSR, 1951.

Gurvich, G.S. and Sokolova, E.V., To the knowledge of relict water bodies of the White Sea, *Tr. Gos. Gidrol. Inst.*, 1939, vol. 15, no. 8, pp. 142–161.

Hammer, O., Harper, D.A.T., and Ryan, P.D., PAST—Palaeontological Statistics, ver. 1.12, 2003. http://folk.uio.no/ohammer/past 2003.

Illyustrirovannye opredeliteli svobodnozhivushchikh bespozvonochnykh evraziiskikh morei i prilezhashchikh glubokovodnykh chastei Arktiki (Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters), vol. 1: *Kolovratki, morskie pauki, rakoobraznye: usonogie, tonkopantsirnye, eufauziidy, nepolnokhvostnye, mizidy, kaprellidy* (Rotifera, Pycnogonida, Crustacea: Cirripedia, Leptostraca, Euphausiacea, Hyperiidea, Mysidacea, and Caprellidea), Sirenko, B.I., Ed., Moscow: Tov. Nauchn. Izd. KMK, 2009.

Illyustrirovannye opredeliteli svobodnozhivushchikh bespozvonochnykh evraziiskikh morei i prilezhashchikh glubokovodnykh chastei Arktiki (Illustrated Keys to Free-Living Invertebrates of Eurasian Arctic Seas and Adjacent Deep Waters), vol. 2: *Nemertiny, golovokhobotnye (priapulidy, kinorinkhi), maloshchetinkovye chervi, piyavki, pogonofory, ekhiury, sipunkuly, foronidy, plechenogie* (Nemertea, Cephalorhyncha, Oligochaeta, Hirudinida, Pogonophora, Echiura, Sipuncula, Phoronida, and Brachiopoda), Buzhinskaya, G.N., Ed., Moscow: Tov. Nauchn. Izd. KMK, 2010.

Izvekova, E.I., Kachanova-L'vova, A.A., and Sokolova, N.Yu., Fauna of the lakes of the Velikii Island and the Kindo Peninsula of the Kandalaksha Bay, the White Sea, in *Biologiya Belogo morya* (The White Sea Biology), Tr. Belomor. Biol. St. Mosk. Gos. Univ., Moscow, 1970, vol. 3, pp. 113–149.

Kharcheva, A.V., Meschankin, A.V., Lyalin, I.I., Krasnova, E.D., Voronov, D.A., and Patsaeva, S.V., The study of coastal meromictic water basins in the Kandalaksha Gulf of the White Sea by spectral and physicochemical methods, *Proc. Int. Soc. Opt. Eng.*, 2014, no. 9031, pp. 1–6.

Khlebovich, V.V. and Aladin, N.V., The salinity factor in animal life, *Herald Russ. Acad. Sci.*, 2010, vol. 80, no. 3, pp. 299–304.

Kompleksnye issledovaniya Bab'ego morya, poluizolirovannoi belomorskoi laguny: geologiya, gidrologiya, biota - izmeneniya na fone transgressii beregov (Integrated Studies of the Bab'e Sea, a Semi-Isolated White Sea Lagoon: Geology, Hydrology, and Biota—Changes against the Background of Coastal Transgression), Tr. Belomor. Biol. St. Mosk. Gos. Univ., Mokievsky, V.O., Isachenko, A.I., Dgebuadze, P.Yu., and Tsetlin, A.B., Eds., Moscow: Tov. Nauchn. Izd. KMK, 2016, vol. 16.

Kosenkov, A.V., Mardashova, M.V., Krylova, M.A., Iz"yurov, I.V., Vinogradov, D.S., and Krasnova, E.D., Quantitative distribution of macrozoobenthos in Lake Trekhtsvetnoe, in *VII Molodezhnyi Kongress po itogam praktik: tezisy dokladov* (VII Youth Congress on the Basis of the Results of Practices, Abstracts of Papers), Moscow, 2015, pp. 179–180.

Krasnova, E.D., Kharcheva, A.V., Milyutina, I.A., Voronov, D.A., and Patsaeva, S.V., Study of microbial communities in redox zone of meromictic lakes isolated from the White Sea using spectral and molecular methods, *J. Mar. Biol. Assoc. U. K.*, 2015, vol. 95, no. 8, pp. 1579–1590.

Krasnova, E.D., Pantyulin, A.N., Rogatykh, T.A., and Voronov, D.A., Inventory of water bodies separating from the sea on the Karelian coast of the White Sea, in *Problemy izucheniya, ratsional'nogo ispol'zovaniya i okhrany prirodnykh resursov Belogo morya* (Problems of Study, Sustainable Use, and Protection of Natural Resources of the White Sea), Petrozavodsk, 2013, pp. 164–167.

Krasnova, E.D., Voronov, D.A., Demidenko, N.A., Kokryatskaya, N.M., Pantyulin, A.N., et al., On the inventory of relict water bodies separating from the White Sea, in *Kompleksnye issledovaniya Bab'ego morya, polu-izolirovannoi belomorskoi laguny: geologiya, gidrologiya, biota izmeneniya na fone transgressii beregov* (Integrated Studies of the Bab'e Sea, a Semi-Isolated White Sea Lagoon: Geology, Hydrology, and Biota—Changes against the Background of Coastal Transgression), Tr. Belomor. Biol. St. Mosk. Gos. Univ., Tov. Nauchn. Izd. KMK, 2016, vol. 12, pp. 211–241.

Kravchunovskaya, E.A. and Gorin, S.L., Formation and dynamics of blocking accumulative forms in the lagoon estuaries of Kamchatka, in *Uchenie o razvitii morskikh beregov: vekovye traditsii i idei sovremennosti: materialy konferentsii* (Doctrine about the Development of Sea Coasts: Age-Old Traditions and Ideas of Our Time: Conference Proceedings), St. Petersburg, 2010, pp. 216–218.

Krylova, M.A., Mardashova, M.V., Iz"yurov, I.V., Kosenkov, A.V., Vinogradov, D.S., et al., Study of the benthic community of the Kislo-Sladkoe Lake in July 2015, in *VII Molodezhnyi Kongress po itogam praktik: tezisy dokladov* (VII Youth Congress on the Basis of the Results of Practices, Abstracts of Papers), Moscow, 2015, pp. 181–182.

Labai, V.S., Atamanova, I.A., Zavarzin, D.S., Motyl'kova, I.V., Mukhametova, O.N., and Nikitin, V.D., *Estestvennaya istoriya Sakhalina i Kuril'skikh ostrovov. Vodoemy ostrova Sakhalin: ot lagun k ozeram* (Natural history of Sakhalin and Kuril Islands. Water Bodies of Sakhalin Island: From Lagoons to Lakes), Yuzhno-Sakhalinsk: GBU kul'tury "Sakhalinskii oblastnoi kraevedcheskii muzei," 2014.

Makarov, A.V., Simakov, M.I., Basin, A.B., and Udalov, A.A., Macrobenthos of the littoral and upper sublittoral of the Bab'e Sea, in *Kompleksnye Issledovaniya Bab'ego morya, poluizolirovannoi belomorskoi laguny: geologiya, gidrologiya, biota izmeneniya na fone transgressii beregov* (Integrated Studies of the Bab'e Sea, a Semi-Isolated White Sea Lagoon: Geology, Hydrology, and Biota—Changes against the Background of Coastal Transgression), Tr. Belomor. Biol. St. Mosk. Gos. Univ., 2016, vol. 12, pp. 144–154.

Mardashova, M.V., Balabin, F.A., Buvaly, S.E., Garmaeva, S.B., Grigorieva, A.A., et al., Investigation of separating sea bays: an integrated approach (bathymetry, structure of the water column, benthic communities, ecology of indicator benthic and terrestrial species) on the model Kislo-Sladkoe and Lower Ershovskoe lakes, in *Abstracts of Lectures and Poster Presentations of the International White Sea Student Workshop on Optics of Coastal Waters, N. Pertsov White Sea Biological Station of MSU, Republic of Karelia, Russia, August 30–September 7, 2014*, Moscow: WSBS, 2014, pp. 23–24.

Mardashova, M.V., Balabin, F.A., Kosenkov, A.V., and Krasnova, E.D., Study of the benthic community of the Kislo-Sladkoe Lake, separated from the White Sea, in winter 2015, in *Bioraznoobrazie nazemnykh i vodnykh zhivotnykh. Zooresursy.: III Vserossiiskaya nauchnaya Internet-konferentsiya s mezhdunarodnym uchastiem: materialy konf. (Kazan', 24 fevralya 2015 g.)* (Biodiversity of Terrestrial and Aquatic Animals. Zoo Resources: Proceedings of III All-Russia Scientific Internet Conference with International Participation, Kazan, February 24, 2015)), PaxGrid Service of Virtual Conferences, Sinyaev, D.N., IE, Kazan, 2015, pp. 41–49.

Mardashova, M.V., Krylova, M.A., Iz"yurov, I.V., Voronov, D.A., and Krasnova, E.D., Study of the benthic community of Nizhnee Ershovskoe Lake in March 2015, in *Sbornik tezisov IV mezhdunarodnoi nauchno-prakticheskoi konferentsii "Morskie issledovaniya i obrazovanie: MARESEDU-2015"* (IV International Scientific-Practical Conference "Marine Research and Education: MARESEDU-2015," Abstracts of Papers), Moscow, 2015a, pp. 84–85.

Mardashova, M.V., Krylova, M.A., Iz"yurov, I.V., Voronov, D.A., and Krasnova, E.D., Study of macrozoobenthos of the lake on Cape Zelenyi in July 2015, in *Sbornik tezisov IV mezhdunarodnoi nauchno-prakticheskoi konferentsii Morskie issledovaniya i obrazovanie: MARESEDU-2015* (IV International Scientific-Practical Conference "Marine Research and Education: MARESEDU-2015," Abstracts of Papers), Moscow, 2015a, pp. 148–150.

Marfenin, N.N., Malyutin, O.I., Pertsova, N.M., Pantyulin, A.N., and Usachev, I.N., *Vliyanie prilivnykh elektrostantsii na okruzhayushchuyu sredu* (The Impact of Tidal Power Plants on the Environment), Moscow: Mosk. Gos. Univ., 1995.

Mokievsky, V.O., Dgebuadze, P.Yu., and Neretin, N.Yu., On the zonality of the Bab'e Sea littoral, in *Kompleksnye issledovaniya Bab'ego morya, polu-izolirovannoi belomorskoi laguny: geologiya, gidrologiya, biota izmeneniya na fone transgressii beregov* (Integrated Studies of the Bab'e Sea, a Semi-Isolated White Sea Lagoon: Geology, Hydrology, and Biota—Changes against the Background of Coastal Transgression). Tr. Belomor. Biol. St. Mosk. Gos. Univ., Moscow: Tov. Nauchn. Izd. KMK, 2016, vol. 12, pp. 154–162.

Mollyuski Belogo morya (Mollusks of the White Sea), Leningrad: Nauka, 1987.

Naumov, A.D., Bottom fauna of Lov Bay (White Sea, Kandalaksha Bay) and its features, in *Ekologiya donnogo naseleniya shel'fovoi zony* (Ecology of the Benthic Population of the Shelf Zone), 1979, pp. 128–136.

Naumov, A.D., *Dvustvorchatye mollyuski Belogo morya. Opyt ekologo-faunisticheskogo analiza* (Bivalves of the White Sea: Experience of Ecological and Faunistic Analysis), St. Petersburg, 2006.

Naumov, A.D. and Martynova, D.M., Summer structure of waters of the Bab'e Sea: comparative analysis of data for two different decades, in *Kompleksnye issledovaniya Bab'ego morya, polu-izolirovannoi belomorskoi laguny: geologiya, gidrologiya, biota izmeneniya na fone transgressii beregov* (Integrated Studies of the Bab'e Sea, a Semi-Isolated White Sea Lagoon: Geology, Hydrology, and Biota—Changes against the Background of Coastal Transgression), Tr. Belomor. Biol. St. Mosk. Gos. Univ., Moscow: Tov. Nauchn. Izd. KMK, 2016, vol. 12, pp. 55–67.

Naumov, A.D., Mokievskii, V.O., Isachenko, A.I., Savchenko, O.N., Biyagov, K.L., and Aristov, D.A., Sublittoral communities of the macrobenthos of the Bab'e Sea, in *Kompleksnye issledovaniya Bab'ego morya, polu-izolirovannoi belomorskoi laguny: geologiya, gidrologiya, biota izmeneniya na fone transgressii beregov* (Integrated Studies of the Bab'e Sea, a Semi-Isolated White Sea Lagoon: Geology, Hydrology, and Biota—Changes against the Background of Coastal Transgression), Tr. Belomor. Biol. St. Mosk. Gos. Univ., Moscow: Tov. Nauchn. Izd. KMK, 2016, vol. 12, pp. 122–143.

Olyunina, O.S. and Romanenko, F.A., Rise of the Karelian coast of the White Sea in the Holocene by the results of the study of peat bogs, in *Materialy V Vseros. soveshch. po izucheniyu chetvertichnogo perioda: "Fundamental'nye problemy kvartera: itogi izucheniya i osnovnye napravleniya dal'neishikh issledovanii"* (Proceedings of the V All-Russia Conference on the Quaternary Study "Fundamental Problems of the Quaternary: The Results of the Study and the Main Directions of Further Research"), Moscow: GEOS, 2007, pp. 312–315.

Opredelitel' fauny i flory severnykh morei SSSR (Keys to Freshwater Invertebrates of Russia and Adjacent Countries), vol. 1: Gaevskaya, N.S., Ed., 1948.

Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territorii (Keys to Freshwater Invertebrates of Russia and Adjacent Countries), vol. 1: *Nizshie bespozvonochnye* (Lower Invertebrates), Tsalolikhin, S.Ya, Eds., St. Petersburg: Nauka, 1994.

Opredelitel' presnovodnykh bespozvonochnykh Rossii i sopredel'nykh territorii (Keys to Freshwater Invertebrates of Russia and Adjacent Countries), vol. 5: *Vysshie nasekomye* (Higher Insects), Tsalolikhin, S.Ya., Ed., St. Petersburg: Nauka, 2001.

Reliktovoe ozero Mogil'noe (issledovaniya 1997-2000 gg.) (Relic Lake Mogilnoe (Studies in 1997–2000)), Murmansk: PINRO, 2002.

Romanenko, F.A. and Shilova, O.S., The postglacial uplift of the Karelian coast of the White Sea according to radiocarbon and diatom analyses of lacustrine-boggy deposits of Kindo Peninsula, *Dokl. Soil Sci.,* 2012, vol. 442, no. 2, pp. 242–246.

Semenov, V.N., *Klassifikatsiya morskikh basseinov boreal'no-arkticheskoi zony: ekologicheskii podkhod* (Classification of Marine Basins in the Boreal-Arctic Zone: An Ecological Approach), Apatity: Karel. Fil. Akad. Nauk SSSR, 1988.

Semenov, V.N., *Sistematika i ekologiya morskikh basseinov Severa na raznykh etapakh izolyatsii* (Systematics and Ecology of Sea Basins of the North at Different Stages of Isolation), Apatity: MMBI, 1988a.

Shaporenko, S.I., Kislo-Sladkie lakes near the Arctic Circle, *Priroda* (Moscow, Russ. Fed.), 2004, no. 11, pp. 23–31.

Shilin, M.B., Kislaya Guva tidal power plant: coming back again and again, *Uch. Zap. Ross. Gos. Gidrometeorol. Univ., Nauchno-Teor. Zh.*, 2009, vol. 11, pp. 101–112.

Sokolov, A.A., *Gidrografiya SSSR* (Hydrography of the USSR), Leningrad: Gidrometeoizdat, 1952. http://www.abratsev.narod.ru/biblio/sokolov/content.html.

Stolyarov, A.P., Macrobenthos of the lagoon ecosystem of the Ermolinskaya Bay (Kandalaksha Bay, White Sea): structural features, diversity and trends of changes, *Vestn. Tver. Gos. Univ., Ser. Biol. Ekol.*, 2016, vol. 4, pp. 130–150.

Stolyarov, A.P. and Mardashova, M.V., Features of the structure and diversity of macrobenthic communities in coastal lagoon ecosystems (Kandalaksha Bay, White Sea), *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 2017, vol. 122, no. 3, pp. 18–27.

Strelkov, P., Shunatova, N., Fokin, M., Usov, N., Fedyuk, M., et al., Marine lake Mogilnoe (Kildin Island, the Barents Sea): one hundred years of solitude, *Polar Biol.*, 2014, vol. 37, no. 3, pp. 297–310.

Subetto, D.A., Shevchenko, V.P., Ludikova, A.V., Kuznetsov, D.D., Sapelko, T.V., et al., Chronology of the isolation of the Solovki Archipelago lakes and the rate of modern lacustrine sedimentation, *Dokl. Akad. Nauk, Ser. Geol.*, 2012, vol. 446, no. 2, pp. 183–190.

Tolomeev, A.P., Shulepina, S.P., Makhutova, O.N., Ageev, A.V., Drobotov, A.V., and Sushchik, N.N., Taxonomic composition and biomass of zoobenthos in saline Lake Shira: shifts that happened in 65 years, *J. Sib. Fed. Univ., Ser. Biol.*, 2018, no. 11 (4), pp. 367–383.

Tsvetkova, N.L., *Pribrezhnye gammaridy severnykh i dal'nevostochnykh morei SSSR i sopredel'nykh vod* (Coastal Gammarids of the Northern and Far Eastern Seas of the USSR and Adjacent Waters), Leningrad: Nauka, 1975.

Ushakov, P.V., *Mnogoshchetinkovye chervi Dal'nevostochnykh morei SSSR (Polychaeta)* (Polychaetes (Polychaeta) of the Far Eastern Seas of the USSR), Moscow: Zool. Inst. Akad. Nauk SSSR, 1955.

Zhirkov, I.A., *Polikhety Severnogo Ledovitogo Okeana* (Polychaetes of the Arctic Ocean), Moscow: Yanus-K, 2001.

Translated by D. Martynova

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